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What the altitudinal and geographical distributions of the Saturniidae along the foothills of the Andes tell us about the so-called pre-Andean zone? (Lepidoptera: Saturniidae)

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Abstract

LEMAIRE & VENEDICTOFF (1989) proposed a biogeographical subdivision of Ecuador based on the distribution of the Saturniidae. Among the various subdivisions, the pre-Andean zone extending from Venezuela to Bolivia results not to be supported by the distribution of the Saturniidae. A critique of their attempt is given according to the absence of endemisms for this altitudinal zone. A detailed analysis of the species listed by LEMAIRE & VENEDICTOFF (1989) as "representative species" for this area is presented accordingly.

KEY WORDS: Lepidoptera, Saturniidae, Biogeography, Andes, area of endemism, speciation, distribution.

¿Qué nos dicen la altitud y distribución geográfica de los Saturniidae a lo largo de las colinas en el pie de monte de los Andes, sobre la llamada zona pre-andina?
(Lepidoptera: Saturniidae)

Resumen

LEMAIRE & VENEDICTOFF (1989) han propuesto una subdivisión biogeográfica del Ecuador basada sobre la distribución de los Saturniidae. Entre las varias subdivisiones, la zona pre-andina se extiende desde Venezuela hasta Bolivia resultados que no están apoyados por la distribución de los Saturniidae. Se da una crítica de estas pruebas, de acuerdo con la ausencia de endemismos para estas zonas altitudinales. Por consiguiente, se presenta un detallado análisis del listado de especies de LEMAIRE & VENEDICTOFF (1989) como "especies representativas" para este área.

PALABRAS CLAVE: Lepidoptera, Saturniidae, biogeografía, Andes, área de endemismos, especiación, distribución.

Introduction

According to the studies conducted by LEMAIRE (1977) and LEMAIRE & VENEDICTOFF (1989), the Saturniidae of Ecuador are faunistically well known if compared with those of other Neotropical countries (RACHELI & RACHELI, 2005a). As LEMAIRE & VENEDICTOFF (1989) pointed out, the Ecuadorian Saturniidae are distributed in four main biogeographical areas. In detail, LEMAIRE & VENEDICTOFF (1989) have subdivided the occidental side of the Andes in an Andean area and a semi-arid zone, but part of this latter is better known as the Tumbesian area of endemism (CRAFT, 1985; BEST & KESSLER, 1995). The oriental side of the Andes was subdivided into two main areas: the Amazonian area and the Andean area. The Amazonian area spans from 250 m to 600 m while the latter was subdivided in three altitudinal zones according to the phytogeographic studies of ACOSTA SOLÍS (1966, 1977): low elevation (or Pre-Andean zone 600-1400 m), moderate elevation,

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subdivided into two further zones: Mesothermic zone (1400-2000 m) and Submesothermic zone (2000-2700 m), and high elevation (2700-3700 m). The fourth area recognized is the Andean Corridor. For each altitudinal subdivision, LEMAIRE & VENEDICTOFF (1989) listed a variable number of "representative species" which are not always endemic species.

In his first biogeographical analysis of the Ecuadorian Saturniids, LEMAIRE (1977) proposed also a Transitional zone between the Andean and Amazonian areas, which spans from 500 m to 1000 m. Later, the same zone was restricted between 600-900 m by LEMAIRE & VENEDICTOFF (1989).

The present paper deals with an analysis of the species of the pre-Andean zone as described by LEMAIRE & VENEDICTOFF (1989) aimed at explaining that their identification of this altitudinal zone is an artifact. Indeed, all the species listed for this zone are not endemic species and the same zone must be likely considered a wider transitional zone between the Andean and the Amazonian biotas. A preliminary issue regarding the identification of two Saturniid areas of endemism is debated.

The artificial pre-Andean zone

The altitudinal range of each pre-Andean species listed by LEMAIRE & VENEDICTOFF (1989) has been re-analysed. Along the eastern side of the Andes from Venezuela to Bolivia, the contact area (600-1400 m) between the Amazonian and Andean biotas was considered a distinct altitudinal zone and named low elevation or the Pre-Andean zone. Firstly, LEMAIRE (1977) listed 15 "representative species" for this area and 13 of these were considered as endemics. Later on, LEMAIRE & VENEDICTOFF (1989) have reduced to five the number of "representative species". According to their altitudinal ranges, none of the five "representative species" listed by LEMAIRE & VENEDICTOFF (1989) for the low elevation (= pre-Andean zone) result to be really endemic to this altitudinal zone except for *Rhescyntis descimoni* Lemaire, 1975 (but see below for further details). Although the altitudinal limits of a given range can be quite variable along the Andes, the absence of true endemisms for the pre-Andean zone frustrates any identification for this altitudinal zone.

Among the five "representative species" listed for the pre-Andean zone, *Arsenura rebeli* Gschwandner, 1920 and *Automeris amanda subobscura* Weymer, 1909 are two Andean species distributed at moderate elevation but with records also from sites situated at low elevation (LEMAIRE & VENEDICTOFF, 1989; RACHELI & RACHELI, 1998a, 1998b). Indeed, *Arsenura rebeli* is an abundant species from 450 to 1800 m while *Automeris amanda subobscura* is more frequent between 1200-1600 m but it has been recorded also at lower elevation although it is still very scarce. The two additional species listed by LEMAIRE & VENEDICTOFF (1989), *Eacles calloptera* Rothschild, 1907 and *Copaxa cineracea* Rothschild, 1895 have been mainly recorded between 600-1400 m but there are records also for higher and/or lower sites (see LEMAIRE, 1988; RACHELI, 1994). *E. calloptera* rather than *C. cineracea* might be considered as a hypothetical pre-Andean endemic species but in any case it is not an endemism of the pre-Andean zone described by LEMAIRE & VENEDICTOFF (1989) because its presence in Venezuela and Colombia has never been confirmed.

A list of further hypothetical pre-Andean species can be arranged but all of them have been recorded only for some of the Andean countries where the pre-Andean zone runs (i.e., from Venezuela to Bolivia). Among them *Copaxa koenigi* Lemaire, 1974 (Ecuador and Peru), *Rachesa adusta* (Rothschild, 1907) (Ecuador and Peru) or *Automeris styx* Lemaire, 1982 (Ecuador, Peru and Bolivia). It seems that the population from French Guyana refers to a different undescribed species) can be considered as hypothetical endemic species of a pre-Andean zone according to their distribution. However, further points must be discussed in detail. Firstly, all the species listed above are known on very few records with *Rachesa adusta* known only on two specimens (RACHELI, 1997). Secondly, all the ranges of these species (or of possible additional species) must be viewed in relationship to the presence of areas of endemism (see the examples below for *A. delormei* and *R. descimoni*). Third, we must also consider if the range of a given species (e.g. *Automeris styx*) is a pre-Andean example or whether it has an Amazonian range with an extension in the transitional area. Not only further researches aimed at increasing the knowledge about the distribution of these species are needed, but in particular the phylogenetic rela-

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tionships of related Andean and Amazonian species will be necessary to have a most complete picture according to a historical framework.

The artificial pre-Andean zone, part II: area of endemism and its historical rule

As noticed above, *Rhescyntis descimoni* has been included by LEMAIRE & VENEDICTOFF (1989) among the five “representative species” for the pre-Andean zone. According to the current range of *Rhescyntis descimoni*, although based on few records only, it is possible to underline that this species is an endemism to a restricted area in eastern Ecuador. The most simple explanation about the range of this taxon refers to the presence of several areas of endemism in Ecuador as recognized for other Lepidopteran lineages (Heliconiinae, Ithomiinae and Papilioninae see review by BROWN, 1987; BROWN *et al.*, 1995). The range of *Rhescyntis descimoni* is congruent with the extension of the area of endemism named Sucua, according to the maximal limits (southern Colombia to north Peru) for species recognized as endemics for this area (BROWN, 1987). However, it must be underlined that the core-area of the Sucua area of endemism is obviously in the Morona-Santiago province. Finally, this taxon cannot be considered as a “representative species” for an altitudinal zone from Venezuela to Bolivia because it is restricted to an area of endemism in eastern Ecuador. The location and extension of this area of endemism on the basis of the distribution of the Saturniidae have not been still identified but two further species, recently described by LEMAIRE (*Periga herbini* Lemaire, 2002 and *Periga extensiva* Lemaire, 2002), supported the presence of a number of endemic species with congruent ranges in this area.

Although a detailed analysis regarding the identification of the Saturniid areas of endemism in the Neotropical region has not been presented, a further example can be useful in explaining the above reasoning about *R. descimoni*. Indeed, the range of *Arsenura delormei* Bouvier, 1929 in Peru and Bolivia is restricted to an altitudinal zone between 600-1200 m. This does not mean that *A. delormei* is a pre-Andean species for the pre-Andean zone as described by LEMAIRE & VENEDICTOFF (1989) inasmuch as the range of this species is congruent with the extension of a wider Chanchamayo area of endemism. The Chanchamayo area of endemism is located in central eastern Peru and it has been identified on the basis of the distribution of Heliconiinae, Ithomiinae and Papilioninae. According to the distribution of Saturniidae (mostly Hemileucinae) but in particular of *A. delormei*, it seems obvious that the identification of an area of endemism in the same area assumes a larger southern extension into Bolivia.

In some ways, the examples for these two unrelated species confirm that their respective ranges and the location of two different Saturniid areas of endemism on the eastern slope of the Andes are congruent. Since areas of endemism are historical units (e. g. CRACRAFT, 1985), the evolutionary histories of these two species (and also their distribution) must be viewed in an historical framework. However, in the absence of phylogenetic analyses for both *Arsenura* and *Rhescyntis* at the lowest categories and not having available a detailed identification of the Saturniid areas of endemism in the Neotropics, further speculations become narrative-based statements hence unwarranted. Moreover, because some of the above arguments about the extension of some areas of endemism have been mainly based on data for diurnal Lepidoptera, it must be pointed out that multiple historical events, and related cycles of area-relationships, did not have influenced in the same way to the diversification and distribution of Saturniidae like in other Lepidopteran lineages (e.g. Heliconiinae, Ithomiinae and Papilioninae). In a different context, this point was also noticed by LEMAIRE & VENEDICTOFF (1989: 8) in their description of the Amazonian region. In this context, it is obvious that both the location and the extension of an area of endemism for Heliconiinae will not be the same for Saturniidae as well as for other lineages (RACHELI & RACHELI, 2004: 349).

Toward an identification of a transitional zone

A further inconsistent explanation given by LEMAIRE & VENEDICTOFF (1989) about their

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view for a pre-Andean zone is based on a series of comparisons on the Saturniid faunas found at two different sites. LEMAIRE & VENEDICTOFF (1989: 7) claimed that the five “representative species” of the pre-Andean zone have been recorded at Lumbaquí (829 m) but not at Lago Agrio (250 m) and also that all the species listed for the latter locality have been also found at Lumbaquí. It seems that this objective result is a further support for their identification of the pre-Andean zone but it is only a questionable point of view for different reasons. Firstly, their statement does not support the existence of a distinct zone only because in the two above sites there are different Saturniid faunas or because the species found in the lowland site are all present also at Lumbaquí. Secondly, four of the five “representative species” are generically considered Andean but not Amazonian species hence their presence at Lago Agrio is *a priori* unexpected. Third, the field expeditions to Lago Agrio have been only a few and the available list of the recorded species for this latter site is an underestimation of the fauna possibly present there. In contrast, a more detailed list of species has been presented for Lumbaquí. At present, all the Saturniid species listed for Lumbaquí by LEMAIRE & VENEDICTOFF (1989) are not under discussion. In any case, it must be pointed out that excluding the specimens collected at Lumbaquí by CLAUDE LEMAIRE and NADIA VENEDICTOFF during their field expeditions to Ecuador, some specimens have been also collected or handled by ROSARIO VELASTEGUI DE LAFEBRE (see for example the presumed female of *Eacles calloptera* figured by LEMAIRE, 1988: pl. 13 fig. 3). This could be a remarkable problem because many of the specimens handled and sold by this collector are wrong labelled (see RACHELI & RACHELI, 2001: 218).

Further, let me consider the following objective example. Among a total of 11 biological species belonging to the genus *Arsenura* listed by LEMAIRE & VENEDICTOFF (1989), eight of them have been recorded at Lumbaquí. The range of these eight species is Guiano-Amazonian or Amazonian except for *Arsenura armida* which is a cosmopolitan species. Secondly, most of these species recorded at Lumbaquí have been subsequently recorded for a typical Amazonian site (Yasuní Natl. Park, Orellana province). What does it mean? Can we affirm that according to the distribution of the *Arsenura* species found at Lumbaquí, this site is in the Amazonian region? The answer is NO. The most logical explanation is that most Amazonian species extend their altitudinal ranges in the foothills of the Andes according to a transitional zone between the Andean and Amazonian biotas. Moreover, a contrary example confirms the present reasoning. As briefly discussed above, *Arsenura rebeli* is a typical Andean species which extends its altitudinal range also to lower elevation. This species has been extensively collected at Misahualli and Puerto Napo (Napo province, Ecuador) but would we affirm that these are Andean sites? The answer is NO, once again. Both these sites show a typical Saturniid fauna characterized by a mixture of Amazonian and Andean species.

In presenting a list of the Saturniid fauna recorded along the Loreto road, RACHELI & RACHELI (1998b) give a similar conclusion also for higher sites in the same province. In that analysis, the Saturniid fauna of various stations located between 1000-1250 m were investigated confirming the sympatric presence of typical Amazonian species [*Arsenura mossi* Jordan, 1922, *Titaea tamerlan amazonensis* Lemaire, 1980, *Procitheronia fenestrata* (Rothschild, 1907)] and Andean species [*Syssphinx bidens* (Rothschild, 1907), *Automeris boops* (Felder & Rogenhofer, 1874) and *Automeris amanda subobscura* Weymer, 1909]. The same conclusion has been given in a recent analysis of the Saturniid communities along an altitudinal transect in the Napo province, Ecuador (RACHELI & RACHELI, 2005b).

The present arrangement for a transitional zone must be viewed as an area where both Andean and Amazonian species expand their distributions possibly according to a post-speciation secondary dispersal. Furthermore, a second but historical explanation could be related to the case where a non-speciation pattern occurred for the majority of the Amazonian Saturniid species according to a non-response to a vicariance event (see also details above and note 3). In any case, the latter conjecture must be discussed having available some phylogenetic hypotheses for Saturniid lineages which include Andean-Amazonian sister species. Then, these hypotheses will be tested in a biogeographical context. At present, it is only possible to record a main Andean-Amazonian pattern of distribution for many Saturniid related species (Racheli, pers. observ.) but their relationships have been arranged only according to an evolutionary systematic arrangement (LEMAIRE, 1996, 2002).

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Epilogue

Finally, there are several objective examples which disconfirm the hypothesis of a pre-Andean zone as described by LEMAIRE & VENEDICTOFF (1989) but confirming the existence of a transitional zone as well as the presence of Saturniid areas of endemism on the eastern slope of the Andes. The above examples are only a few but they are enough in supporting the latter statements. A natural pre-Andean Saturniid fauna is not therefore well supported by the recognition of congruent ranges of Saturniid species. In fact, the “representative species” listed by LEMAIRE & VENEDICTOFF (1989) should not be considered as endemic and this altitudinal zone is constituted by a mixture of Amazonian and Andean species. It is better to consider this altitudinal belt as a transitional zone between 450 to 1200 m according to the altitudinal distribution of the Saturniidae. Lastly, it seems a paradox but I must admit that LEMAIRE & VENEDICTOFF (1989: 7-8) are contradictory when describing their Amazonian region claimed that the Amazonian Saturniid fauna spreads up also to 1400 m along the foothills of the Andes. They seem to be in agreement with me but not with their pre-Andean zone as described only few lines before.

Acknowledgements

Originally, all the basic arguments discussed in the present paper were written during 1997-1998 but for different reasons never finished. When I was back on my manuscript in the spring 2005, Dr. Claude Lemaire was unfortunately passed away and he will never reply to my criticisms. In any case, I am convinced that a revision of his biogeographical subdivision is needed and any hypothetical advocates of the Lemaire's view would reply to that present above. Although I disagree with him in different ways, the monumental efforts to the knowledge of the Neotropical Saturniidae given by Lemaire during his life are unquestionable.

My unforgivable delay in finishing the present article was also due to the spurious comments or lacking of criticisms received on preliminary versions of this paper. Finally, I am grateful to Tommaso Racheli for his valuable suggestions which improved the text. I take full responsibility about the arguments debated above.

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